PLIOCENE RODENTS OF WESTERN NORTH AMERICA

INTRODUCTION

Knowledge concerning the extinct mammal faunas of North America has increased enormously since the beginning of the present century. Certain groups of mammals are known in great detail and fairly satisfactory "trees" showing their phylogenetic relationships have been erected. Other groups are not so well known, but the general course of their history has been traced and little remains but to fill in the gaps and to make minor corrections. On the other hand, a few groups have proved more or less refractory, and the order Rodentia may be regarded as one of the more important of these. Not only are the broader phases of rodent evolution, such as the differentiation of modern families from ancestral stocks, not at all well known, but it is commonly assumed that rodent types are remarkably stable, the same genus, and even species, having an extremely long range in geologic time as compared with those grouped under other orders. Hence the rodents at present are regarded by many as an order offering but little from an evolutionary standpoint, and as barred by their stability from any use in detailed stratigraphy and correlation.

The views expressed above are those held by most palæontologists. They are, however, views inherited for the most part from older workers, handicapped by lack of sufficient material and knowledge of the stratigraphic location of that material. Most present-day workers on fossil rodents, although not agreeing among themselves as to the limiting possibilities of rodent research, feel that the older views are not altogether correct.

Before proceeding to a discussion of the scope of the present paper, it seems pertinent to outline briefly the various lines of rodent research and the advances made thus far, as well as to indicate the results which may be expected from a study of fossil rodents.

Some of the more fundamental types of research relate to the differentiation of modern families from a common rodent stock. At present, extremely little is known and widely divergent views are held with regard to the time and manner of that differentiation. If results are to be obtained in this direction, it will be particularly through a careful study of middle and upper Eocene rodents. A study of all material now available probably would extend our knowledge demonstrating the Eocene ancestry of the modern families. It is likely, however, that final proof will have to await the discovery of more perfect specimens and the acquisition of more extensive upper Eocene rodent

faunas. One of the chief drawbacks to any work on the differentiation of modern families lies in the absence of skull material from critical horizons. This view appears more likely to account for the lack of intermediate types than the alternative one, presented by Miller and Gidley (1918), that the Rodentia were already differentiated at the time of their first appearance in the palæontological record.

A second direction of research is the establishment of phylogenetic lines within the family. Fossil materials known at the present time are hardly sufficient for detailed phylogenetic studies. They suffice in most cases to establish the broad lines of evolution, or at least to suggest such lines.

A third field of investigation is concerned primarily with the description of rodent faunas from various stages. This type of research has value in enlarging our picture of the past mammalian life, and in furnishing a basis for study in the previously mentioned fields. At present even this work is neglected, and large collections of undescribed rodents are in existence. Omission of studies of this kind has proved a stumbling block for more ambitious projects along other lines. Of course in connection with such investigations phylogenetic studies should not be neglected.

An outgrowth of faunal studies is the recognition of the time range of various genera and species, and the establishment of important index fossils. With increasing knowledge of fossil rodents it has become apparent that certain groups, at least, will ultimately furnish distinctive horizon markers. At present the number of such index fossils is few. However, if the existing rodents, which embrace more different types than all other mammals combined, have descended as commonly believed from a single lower Eocene genus or at most from several closely related genera, it is obvious that the Tertiary radiation is very great, and consequently the group should furnish many such markers.

The nature of the present paper practically limits the fields of discussion to the last two mentioned above. All present-day families were established long before the opening of Pliocene time. The short duration of that epoch, as well as the fragmentary nature of the material, sharply limit the observable evolution of the order during that time. Pliocene rodent assemblages are not very abundant nor are they complete, but this is likewise true of other mammalian remains from the epoch, so that any data which may be obtained as to the stratigraphic position of faunas are relatively more important than similar data for other divisions of the Tertiary.

The term Pliocene is here used to include not only all true Pliocene occurrences but also the doubtful Miocene-Pliocene and Pliocene-Pleistocene faunas. In a general way this covers a period embraced

by the European time sequence, Pontian to Sicilian. The present paper deals only with Pliocene faunas from western North America, but since no Pliocene rodent types have been recorded elsewhere in North America, the study is not actually limited geographically.

This review is the result of studies that have been made on Pliocene rodent faunas from: (1) Kern River beds of California; (2) Smiths Valley, Nevada; (3) Rome, Oregon; (4) Coso Mountains, California; (5) Hagerman, Idaho; and (6) Grand View, Idaho. During the course of the work, examination was also made in whole or in part of faunas from the following localities: (1) Bartlett Mountain, Oregon; (2) Fish Lake Valley, Nevada (Esmeralda fauna of Stirton); (3) Rattlesnake, Oregon; (4) Thousand Creek, Nevada; and (5) San Pedro Valley, Arizona (Curtis fauna). Other Pliocene rodent collections are known to the author only through published descriptions. Detailed accounts of faunas in the California Institute of Technology collections have already been published (Wilson, 1932, 1933, 1934, 1935, 1936, and 1937).

While lack of familiarity with certain faunas, especially those of the Great Plains Pliocene, has served to restrict observations on several phases of the work, it is hoped that the succeeding pages will help to bring together widely separated data on Pliocene Rodentia. The treatment is faunal rather than taxonomic, and, moreover, represents only a progress report, inasmuch as any final statement must rest on the acquisition of more extensive collections.

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PREVIOUS STUDIES OF NORTH AMERICAN FOSSIL RODENTS

Early workers in the field of North American fossil rodents were first Joseph Leidy, followed by E. D. Cope, O. C. Marsh, and finally W. D. Matthew. Other palæontologists contributed, to be sure, but by far the bulk of the work was carried on by these four men. Their investigations covered a period extending from the first studies of Leidy down to 1910. It was mainly a period of description with little or no attempt to outline phylogenetic trends. It is true that relationships of various extinct types of rodents to modern forms were recognized, sometimes with surprising accuracy considering the poor material available for study. On the other hand, we find identifications of John Day lagomorphs as *Lepus,* lower Oligocene ischyromyids as *Sciurus,* and John Day castorids as *Castor.* Perhaps it was such identifications that established the belief that rodents were extremely stable forms.

It is difficult to evaluate the importance of the work by Leidy, Cope, and Marsh, and the earlier studies of Matthew. Leidy, publishing chiefly in the proceedings of the Academy of Natural Sciences of Philadelphia and in various government reports, commands attention principally because his work was the starting point for later, more comprehensive studies. Cope was probably the dominant figure of the first period of rodent research in this country. His researches are summarized in "The Vertebrata of the Tertiary Formations of the West" (1884). Marsh's contribution is relatively unimportant as compared with that of the other three palæontologists. His most important work was in connection with the building of a large collection of Bridger rodents which apparently has never been completely described or even prepared for study. With Cope's death, Matthew became the leading worker in the field. Practically all his contributions are to be found in the various publications of the American Museum.

The modern period of fossil rodent research may be dated from the publication by Matthew, in 1910, of his classic contribution "On the Osteology and Relationships of Paramys, and the Affinities of the Ischyromyidæ." The view expressed in this paper that the order of rodents is descended from a *Paramys* or *Paramys*-like ancestor of the lower Eocene is accepted at present by most workers in the field of rodent palæontology. The only exception taken to this concept by American workers was made in 1918 by Miller and Gidley in their "Synopsis of the Supergeneric Groups of Rodents." This paper was originally intended as a preliminary report on an ambitious program of study of the entire field of fossil and living rodents. The final report has never been published. The synopsis presented many new ideas, extremely discouraging to further rodent work if they could be

proved. As has been pointed out at various times by several palæontologists, this paper is more an artificial key for the recognition of supergeneric or family groups than a genetic classification. The principal view presented by Miller and Gidley, as mentioned previously, is that all rodent families were completely differentiated at the time of their first appearance in the palæontological record.

A more recent phase of the modern period has been research on family or subfamily groups of rodents. Here might be mentioned one European work: Schaub's "Die hamsterartigen Nagetiere des Tertiärs" (1925), which is perhaps the first accurately written and accurately illustrated publication dealing with the evolution of a phylum of rodents. Recent American publications of this type have been: "Evolution and Relationship of the Heteromyid Rodents," by A. E. Wood (1935), and "A Review of the Tertiary Beavers," by R. A. Stirton (1935).

A review of the literature dealing exclusively with Pliocene rodents is difficult to present. Most of the work accomplished to date has been in connection with descriptions of other mammals. Papers dealing exclusively with Pliocene rodents are limited in number. In 1910, Miss Louise Kellogg published a description of a "Rodent Fauna of the Late Tertiary Beds at Virgin Valley and Thousand Creek, Nevada." J. W. Gidley's "Preliminary Report on Fossil Vertebrates of the San Pedro Valley, Arizona, with Descriptions of New Species of Rodentia and Lagomorpha" appeared in 1922. More recently, in 1930, E. Raymond Hall issued a report on the "Rodents and Lagomorphs from the Later Tertiary of Fish Lake Valley, Nevada." Lastly, several papers by the present author concerning Pliocene rodents have been presented from time to time since 1932. The bibliography lists these publications (1932, 1933, 1934, 1935, 1936, and 1937).

THE NATURE OF NORTH AMERICAN TERTIARY RODENT FAUNAS

TAXONOMIC CLASSIFICATION

The taxonomic classification of rodents used in this paper is in no sense original. Perhaps it is closest to Simpson's arrangement presented in 1931. Certain changes have been made where such changes appear desirable to the author or where a compromise with several systems seems advantageous. The present arrangement has the advantage or disadvantage, depending on the point of view, of being very conservative. The following outline omits families not recorded from North America, as well as the families Dipodidæ and Muridæ, which have been doubtfully recorded. It is intended principally as a

guide to later discussions concerning particular families and their representatives.

Order Rodentia (rodents in a strict sense)
- Suborder Sciuromorpha (squirrel-like rodents)
  - Superfamily Aplodontoidea
    - *† Family Ischyromyidæ
    - † Family Mylagaulidæ
    - Family Aplodontiidæ (mountain-beavers or sewellels)
  - Superfamily Sciuroidea
    - Family Sciuridæ (squirrels)
  - Superfamily Castoroidea
    - Family Castoridæ (beavers)
  - Superfamily Geomyoidea
    - Family Heteromyidæ (pocket-mice and kangaroo-rats)
    - Family Geomyidæ (pocket-gophers)
- Suborder Myomorpha (mouse-like rodents)
  - Superfamily Myoidea
    - Family Cricetidæ (rats and mice)
  - Superfamily Dipodoidea
    - Family Zapodidæ (jumping-mice)
- Suborder Hystricomorpha (porcupine-like rodents)
  - Superfamily Hystricoidea
    - Family Erethizontidæ (New World porcupines)
    - * Family Caviidæ (guinea-pigs)

Order Lagomorpha (rabbits, hares, and pikas)
- Family Ochotonidæ (pikas)
- Family Leporidæ (rabbits and hares)

* Not present in Pliocene.
† Extinct.

The popular term rodent embraces two orders of mammals which may have only a very distant relationship. One order, the Lagomorpha, which includes the hares, rabbits, and pikas, is a rather restricted group and has remained remarkably stable from its first appearance in the fossil record. The second order, that of the Rodentia, or true rodents, is marked by an extreme diversity of type originating from a central stock. These forms consequently exhibit parallelism among themselves to an extraordinary degree. The present study will include both orders, since the Lagomorpha are so limited as to make separate treatment not very desirable.

The classification of the Rodentia used here is the old threefold division, namely, the Sciuromorpha or squirrel-like rodents, the Myomorpha or mouse-like rodents, and the Hystricomorpha or porcupine-like rodents, based principally on the character of the masseter muscle and its attachment to the skull. This division is not universally accepted or entirely satisfactory, but in the case of North American rodents it is a fairly logical one and very convenient. The North American sciuromorphs include the mountain-beavers,

squirrels, beavers, gophers, pocket-mice, and kangaroo-rats among living forms, and the ischyromyids and mylagaulids among extinct types. These forms are characterized by relatively small infraorbital foramina in which no invasion by the masseter muscle takes place. Moreover, the angle of the ramus appears to originate on the inferior border of the ramus, and not upon the side as in the Hystricomorpha.

Only two families of North American myomorphs have been definitely recorded, namely the Cricetidæ, including indigenous rats and mice, and the Zapodidæ or jumping-mice. In these forms the infraorbital foramen becomes enlarged and is traversed by a branch of the masseter muscle. The angle of the ramus is similar to that of the Sciuromorpha.

The North American Hystricomorpha include representatives of the Erethizontidæ or porcupines, and the Caviidæ or guinea-pigs. In these forms the infraorbital foramen is extremely large and transmits the masseter medialis. The angle of the ramus appears to originate on the side of the ramus, in contrast with the more normal angle of the Sciuromorpha and Myomorpha. This group is relatively unimportant among North American rodents. Our only known forms are invaders from South America.

SCIUROMORPH PREDOMINANCE IN NORTH AMERICA

The Sciuromorpha is the most primitive of the suborders, and probably gave rise to the other two. In North America it is the dominant group of the Tertiary. All sciuromorph families are represented excepting the anomaluroids. The mylagaulids, gophers, and heteromyids are confined to North America, and the aplodontids are represented elsewhere only by a single Pliocene specimen from Asia.

In the ascendancy of the sciuromorphs, North America stands in contrast to most other continents, in which, during the Miocene and Pliocene at least, the higher types of Rodentia are the dominant types. In Asia most of the later Tertiary forms are myomorphs; in South America the fauna is almost exclusively hystricomorph. For these reasons study of North American rodents is limited essentially to the Sciuromorpha. Studies concerning the evolution of the Aplodontiidæ, Mylagaulidæ, Geomyidæ, and Heteromyidæ should furnish, and are furnishing, important data on the evolution of these families, since the groups mentioned are virtually confined to this continent. North American fossil Myomorpha may yield a limited amount of data on certain members of the Cricetidæ and Zapodidæ, but the seat of higher rodent evolution is elsewhere. The date of appearance of certain hystricomorph types may eventually afford horizon markers, but the evolution of this group occurred farther to the south.

PLIOCENE RODENT FAUNAS

The relative position of most of our Pliocene faunas is more or less agreed upon. However, there is wide divergence of view as to where the Miocene-Pliocene and Pliocene-Pleistocene boundary lines should be drawn. Consequently, unless one makes clear what is meant by lower Pliocene, for example, considerable confusion may arise. The lower Pliocene of one author may include the Thousand Creek, of another the Fish Lake Valley beds. To say that the extinct beaver *Eucastor* is characteristic of the lower Pliocene is ambiguous if the statement is not accompanied by a qualifying explanation, since the characteristic Thousand Creek beaver is *Dipoides*.

In the present paper a threefold division of the Pliocene into lower, middle, and upper is adopted. The lower division includes such faunas as the Fish Lake Valley or Esmeralda, which would be considered upper Miocene or perhaps transitional by some authorities. It is roughly equivalent to the so-called Pontian faunas of Europe and Asia. The author expresses no particular convictions in placing the faunas assigned to this division in the lower Pliocene instead of the upper Miocene, but it seems a rather convenient arrangement. As a matter of fact, if the extreme views of some authors were applied to the lower and upper boundaries of the Pliocene, this period would be reduced almost to the vanishing point. In any case, the placing of boundary lines is frequently an academic question not always consistent with the facts of Nature.

The middle Pliocene of this paper includes such faunas as the Thousand Creek, Rattlesnake, and upper Snake Creek. The Pliocene age of these faunas is agreed upon by all American palæontologists. They are roughly comparable to the Plaisancian faunas of Europe.

The division termed upper Pliocene includes faunas from Grand View, Hagerman, the upper Etchegoin, and San Pedro Valley. These faunas correspond in part to the lower Pleistocene of some authors. Their European equivalents are the Norwich Crag and Val d'Arno. There seems some justification for the belief that at least part of the present author's upper Pliocene should be termed lower Pleistocene. This question will be discussed in some detail in a later and more convenient place.

The following rodent faunal lists are as complete and accurate as it is possible to make them. Determinations have been brought up to date whenever feasible, and some genera of doubtful presence eliminated. It is extremely difficult to give accurate lists for the Great Plains Pliocene faunas, since considerable reworking of materials and indistinct contacts seem to be characteristic of these deposits. Moreover, the exact locality of many types is not known, since the collecting of these specimens occurred in the days when ac-

curate location of materials was not made. Rodent faunas that are too poorly known and possess no particular importance are omitted.

LOWER PLIOCENE

Fish Lake Valley Fauna (Esmeralda of Stirton)

Locality—Fish Lake Valley, Esmeralda County, Nevada.

Rodentia
- Family Mylagaulidæ
  - *Mylagaulus* sp. (cf. *monodon* Cope)
- Family Castoridæ
  - *Eucastor dividerus* Stirton
- Family Heteromyidæ
  - *Perognathoides tertius* (Hall)
  - *Perognathoides quartus* (Hall)
- Family Cricetidæ
  - *Peromyscus dentalis* Hall
  - *Macrognathomys nanus* Hall

Lagomorpha
- Family Leporidæ
  - *Hypolagus* cf. *vetus* (Kellogg)
  - *Sylvilagus?* sp.

In the original description of the fauna, E. Raymond Hall (1930) figured an isolated tooth which he doubtfully referred to the Geomyidæ. Hall tentatively identified the specimen as *Entoptychus?* sp. Recently, A. E. Wood (1936a) has suggested that the fragment is probably a deciduous upper premolar of a lagomorph.

Siesta Formation

Locality—Berkeley Hills, California.

Rodentia
- Family Castoridæ
  - *Eucastor lecontei* (Merriam)

Lagomorpha
- Family Leporidæ
  - *Lepus* sp.

The reference of lagomorph material to *Lepus* by J. C. Merriam is probably incorrect. Since there is no published description of the material, the original designation is retained, but the form represented is probably *Hypolagus* or some similar type.

Valentine Beds

Locality—Valentine, Nebraska.

The Valentine beds are usually designated as upper Miocene, lower Pliocene, or transitional. Recent work has indicated that more than

one faunal horizon is present, and the older faunal lists are presumably of composite nature. Johnson (1936) and Stirton and McGrew (1935) agree that at least two faunas can be distinguished. The older is apparently of upper Miocene or transitional age, and antedates any other fauna listed as lower Pliocene in this paper. The name Valentine fauna has been applied to this assemblage by Johnson, and Niobrara River by Stirton and McGrew. Since the present author is in no position to judge the merits of either name, and since Valentine has been adopted by most palæontologists including those of the Nebraska Geological Survey and the Nebraska State Museum, this term will be used in the present paper. The younger fauna has been designated the Burge fauna by Stirton and McGrew, and the name was subsequently adopted by Johnson. The latter author has termed the beds carrying the Burge fauna, the Burge sands. According to Stirton and McGrew (1935, p. 129), the Burge fauna appears to be equivalent to the Fish Lake Valley assemblage.

Until the Valentine and Burge faunas are revised and restudied in detail in the light of more recent knowledge, rodent faunal lists of these assemblages are to be regarded as tentative. The Valentine rodent fauna presented below is probably in part composite, but is listed for completeness. Starred (*) forms are presumably from the "type" quarries of the Valentine.

Valentine Fauna

Rodentia
- Family Mylagaulidæ
  - *Mylagaulus "monodon"* Cope
- Family Castoridæ
  - * *Monosaulax pansus* (Cope)
  - * *Monosaulax curtus* (Matthew and Cook)
  - * *Monosaulax* or *Eucastor* sp.
  - *Eucastor* cf. *tortus* Leidy
- Family Heteromyidæ
  - * *Cupidinimus nebraskensis* Wood
  - * ?*Diprionomys* sp. nov. indet. (determination by Wood)
  - * Heteromyid sp. (an undescribed form related to *Microdipodops*, U. C. Coll.)
  - *Diprionomys agrarius* Wood (Devil's Gulch beds, *Teleoceras* level)
- Family Geomyidæ
  - ?*Geomys bisulcatus* Marsh (listed by Cook and Cook, 1933)

Lagomorpha
- Some remains recorded

Burge Fauna

Rodentia
- Mylagaulidæ
  - *Mylagaulus* sp.
- Castoridæ
  - *Eucastor* sp.

MIDDLE PLIOCENE

Bartlett Mountain Fauna

Locality—Bartlett Mountain, near Drewsey, Harney County, Oregon.

Rodentia
- Family Mylagaulidæ
  - *Mylagaulus* cf. *monodon* Cope
- Family Sciuridæ
  - Citellid sp.
- Family Castoridæ
  - *Dipoides?* sp.
- Family Geomyidæ
  - Geomyid? sp.

Lagomorpha
- Family Leporidæ
  - Leporid sp.

The Bartlett Mountain fauna is an undescribed assemblage in the collections of the California Institute of Technology. It was discovered by Chester Stock and E. L. Furlong in 1928.

Rattlesnake Formation

Locality—Dayville, Grant County, Oregon.

Rodentia
- Family Sciuridæ
  - *Otospermophilus gidleyi* Merriam, Stock, and Moody
- Family Castoridæ
  - *Dipoides* sp.

Lagomorpha
- Family Leporidæ
  - *Hypolagus* near *vetus* (Kellogg)

W. D. Matthew (1933) has objected strenuously to referring the Rattlesnake citellid to the Recent subgenus *Otospermophilus*. Most of his very cogent remarks were based on characters exhibited in *Sciurus angusticeps*, a middle Miocene or lower upper Miocene specimen from the Deep River beds. It is possible, however, that in view of the considerably later age of *Otospermophilus gidleyi*, the genus *Citellus* was sufficiently differentiated to have distinct representatives of its subgenera in existence. I am inclined to agree with the view expressed by Matthew, since none of the middle Pliocene representatives of *Citellus* which I have seen appears to have progressed beyond a *Callospermophilus* or *Otospermophilus*-like stage in the dentition. As a matter of fact, Dr. Gidley, when describing the specimen for Merriam, Stock, and Moody, regarded its reference to *Otospermophilus* as tentative.

Kern River Deposits

Locality—Bakersfield Quad., U. S. Geol. Surv., N.E. ¼ Sec. 26, T. 28 S., R. 28 E., Mt. Diablo Base and Mer., Kern County, California.

Rodentia
- Family Sciuridæ
  - *Citellus?* sp.
- Family Cricetidæ
  - *Peromyscus pliocenicus* Wilson

Lagomorpha
- Family Leporidæ
  - *Hypolagus* near *limnetus* Gazin
  - *Hypolagus* small sp.

This fauna has been described in a recent publication entitled "New Middle Pliocene Rodent and Lagomorph Faunas from Oregon and California" (Wilson, 1937).

Smiths Valley Fauna

Locality—Smiths Valley, Lyon County, Nevada.

Rodentia
- Family Aplodontiidæ
  - Aplodontid sp.
- Family Sciuridæ
  - *Citellus?* sp.
- Family Geomyidæ
  - *Pliosaccomys dubius* Wilson
- Family Cricetidæ
  - *Peromyscus* near *antiquus* Kellogg
- Family Zapodidæ
  - *Pliozapus solus* Wilson

Lagomorpha
- Family Leporidæ
  - Leporid sp.

The Smiths Valley rodent assemblage has been described recently by the author (1936).

Thousand Creek Beds

Locality—Thousand Creek, Humboldt County, Nevada.

Rodentia
- Family Mylagaulidæ
  - *Mylagaulus* cf. *monodon* Cope
- Family Aplodontiidæ
  - *Liodontia furlongi* Gazin
- Family Sciuridæ
  - *Marmota nevadensis* (Kellogg)
  - *Marmota minor* (Kellogg)
  - *Citellus* sp.

Family Castoridæ
Dipoides sp.
Family Heteromyidæ
Diprionomys parvus Kellogg
Cupidinimus magnus (Kellogg)
Family Cricetidæ
Peromyscus antiquus Kellogg
Lagomorpha
Family Leporidæ
Hypolagus vetus (Kellogg)

Liodontia furlongi was described originally by E. L. Furlong (1910) as *Aplodontia alexandræ*. The latter species included specimens from both Virgin Valley and Thousand Creek. Subsequently, Miller and Gidley (1918, p. 440) made *A. alexandræ* the type of a new genus, *Liodontia*. Finally, C. L. Gazin (1932, pp. 64–65) separated the Thousand Creek specimens of *alexandræ* as a distinct species, *L. furlongi*.

The rodent species described by Miss Kellogg (1910) as *Entoptychus minimus* has been referred to the genus *Diprionomys* by A. E. Wood.[1] Wood considers *D. minimus* as "a previously unknown species of *Diprionomys*." It is possible that *D. minimus* is synonymous with *D. parvus* from the same beds, and that it represents a relatively unworn dentition of the latter species. $P\overline{4}$ of *D. parvus*, although very close in pattern to the comparable tooth in *D. minimus*, seems much larger. However, difference in stage of wear may account for this difference in size. (1) Jaws are approximately of same size. (2) The teeth of *D. minimus* do not fill their alveoli, an indication that they have not attained their maximum size. Moreover, $P\overline{4}$ appears to widen toward its base. (3) If *Diprionomys* is a heteromyine, it should be noted that in the genus *Liomys* $P\overline{4}$ progressively increases in area of wearing surface as the tooth is worn.

Cupidinimus magnus was described originally as *Diprionomys magnus*. The species was transferred to the present genus by A. E. Wood (1935).

Rome Fauna

Locality—Rome, Malheur County, Oregon.

Rodentia
Family Mylagaulidæ
Mylagaulus? cf. *monodon* Cope
Family Castoridæ
Dipoides stirtoni Wilson
Castor? sp.

[1] A. E. Wood, Fossil Heteromyid Rodents in the Collections of the University of California, (abstract) Preliminary List of Titles and Abstracts, 48th Ann. Meeting G. S. A., 1935; Amer. Mus. Nov., No. 866, 24–25, 1936.

Family Cricetidæ
Goniodontomys disjunctus Wilson
Lagomorpha
Family Leporidæ
Hypolagus vetus (Kellogg)
Hypolagus sp.

There may be some doubt as to the association of the *Castor?* species with the remaining rodent fauna. The occurrence of the specimen in an area isolated from that in which the other rodents were obtained, and the presence of beds of possible upper Pliocene or Pleistocene age in the vicinity, raise this question. However, the association in the field of *Castor?* with *Pliohippus* teeth and the characters exhibited by the specimen itself obviate this possibility to a large extent.

This fauna has been recently described by the author (1937).

Upper Snake Creek Beds

Locality—About twenty miles south of Agate, Sioux County, Nebraska.

Rodentia
Family Mylagaulidæ
Mylagaulus monodon Cope
Mylagaulus sesquipedalis Cope
Family Sciuridæ
Sciurus cf. *aberti* Woodhouse
Family Castoridæ
Eucastor cf. *tortus* Leidy
Eucastor sp.
Dipoides prob. n. sp. (according to Stirton)
Castor cf. *californicus* Kellogg
Family Heteromyidæ
Perognathus coquorum Wood
Family Geomyidæ
? *Thomomys* sp.
? *Geomys* sp.

As in the case of the Valentine, the upper Snake Creek beds of the Great Plains possess apparently a mixed fauna. The rodent assemblage given above seems also to include forms coming from several ages. Noticeably is this so in the presence of both *Eucastor* and *Dipoides,* especially with associated *Castor.* Among the Geomyidæ I have listed both *Geomys* and *Thomomys.* Both genera are sometimes given as occurring in the upper Snake Creek beds, but apparently this is an error. Matthew in 1924 (p. 66) lists only *Thomomys,* known by a single ramus without teeth. Matthew in an earlier contribution to the Snake Creek faunas mentioned the presence of *Geomys* as evidenced by a lower jaw without dentition. Probably a

single specimen has accounted for both determinations, and the later assignment is Matthew's final opinion on the specimen.

While the upper Snake Creek rodent assemblage has been given, its apparent composite nature militates against its use in correlation, and the fauna is listed only for the sake of completeness.

Edson Beds

Locality—Near Edson, Sherman County, Kansas.

Rodentia
- Incertæ sedis
  - *Kansasimys dubius* Wood
- Family Mylagaulidæ
  - *Mylagaulus monodon* Cope
- Family Sciuridæ
  - *Sciurus* sp.

The genus *Kansasimys* Wood cannot be assigned very well to any known family of rodents. Moreover, as A. E. Wood (1936b) has mentioned, it does not seem advisable to erect a new family for its reception. On the basis of dental characters, this genus might be assigned to the Ischyromyidæ of the present paper, since it possesses characters found in one or another of the varied early Tertiary types which are designated here collectively as the Ischyromyidæ. However, the forward extension of the masseteric fossa in the jaw of *Kansasimys* would prohibit allocation of the genus to this family. Little else than the primitive development of the masseter muscle is shared in common by the genera grouped by W. D. Matthew under the Ischyromyidæ.

UPPER PLIOCENE

Upper Etchegoin Formation (San Joaquin Clay)

Locality—Southwestern San Joaquin Valley, California.

Rodentia
- Family Castoridæ
  - *Castor californicus* Kellogg
- Family Cricetidæ
  - *Mimomys primus* (Wilson)

Castor californicus is recorded from the Kettleman Hills, and *Mimomys primus* from the Buttonwillow gas field, some distance away. However, the stratigraphy of the west side of the San Joaquin Valley is rather well known and the specimens both come from the San Joaquin clay. According to Barbat and Galloway (1934), *Mimomys* is from a higher zone (zone B) than *Castor* (zone C).

Coso Mountains Fauna

Locality—Coso Mountains, Inyo County, California.

Rodentia
- Family Cricetidæ
  - *Mimomys primus* (Wilson)

Lagomorpha
- Family Leporidæ
  - *Hypolagus* near *limnetus* Gazin
  - *Hypolagus* small sp.

Contributions to the mammalian fauna of the Coso Mountains have been made by Stock, Wilson, and Schultz. J. R. Schultz is now preparing a complete statement of the fauna and its faunal and age relationships.

Hagerman Lake Beds

Locality—Hagerman, Twin Falls County, Idaho.

Rodentia
- Family Sciuridæ
  - *Citellus?* sp.
  - Marmot sp. (Gazin, 1936, p. 285)
- Family Castoridæ
  - *Castor* sp. (On the whole, intermediate between *C. californicus* and *C. canadensis*, according to Stirton, 1935, pp. 446–447)
- Family Geomyidæ
  - *Thomomys gidleyi* Wilson
- Family Cricetidæ
  - *Mimomys primus* (Wilson)
  - *Ondatra idahoensis minor* Wilson

Lagomorpha
- Family Leporidæ
  - *Hypolagus* near *vetus* (Kellogg)
  - *Hypolagus limnetus* Gazin
  - *Alilepus? vagus* Gazin

The marmot and beaver material was not examined by the present author.

Grand View Fauna, Idaho Formation (?)

Locality—Near Grand View, Owyhee County, Idaho.

Rodentia
- Family Castoridæ
  - *Castor* cf. *accessor* Hay
- Family Cricetidæ
  - *Synaptomys vetus* Wilson
  - *Mimomys? parvus* Wilson
  - *Ondatra idahoensis idahoensis* Wilson
- Family Erethizontidæ
  - *Erethizon bathygnathum* Wilson

Lagomorpha
Family Leporidæ
Hypolagus furlongi Gazin

Both the Grand View and Hagerman faunas come from beds which in the past have been called the Idaho formation. C. L. Gazin in various papers on the Hagerman fauna has referred to the beds near Hagerman as the Hagerman lake beds. The two faunas are probably separated somewhat in time, the Hagerman fauna being slightly older.

Benson Fauna (San Pedro Valley Beds)

Locality—Near Benson, Cochise County, Arizona.

Rodentia
Family Sciuridæ
Citellus bensoni Gidley
Family Heteromyidæ
Dipodomys minor Gidley
Cupidinimus magnus (Kellogg)
Family Geomyidæ
Geomys minor Gidley
Cratogeomys bensoni Gidley
Family Cricetidæ
Peromyscus brachygnathus Gidley
Peromyscus minimus Gidley
Eligmodontia arizonæ Gidley
Onychomys bensoni Gidley
Sigmodon medius Gidley
Neotoma fossilis Gidley
Lagomorpha
Family Leporidæ
Lepus, 2 sp.
Sylvilagus or *Brachylagus* sp.

Curtis Fauna (San Pedro Valley Beds)

Locality—Near Benson, Cochise County, Arizona.

Rodentia
Family Sciuridæ
Citellus cochisei Gidley
Family Heteromyidæ
Perognathus sp.
Dipodomys minor Gidley
Dipodomys gidleyi Wood
Family Geomyidæ
Geomys persimilis Hay
Family Cricetidæ
Onychomys pedroensis Gidley
Sigmodon curtisi Gidley
Sigmodon minor Gidley
Neofiber? sp.
Lagomorpha
Family Leporidæ
Lepus sp.

Neofiber? species, known from an incomplete upper molar, appears to be generically distinct from *Neofiber* in possessing rooted cheek-teeth. Perhaps the specimen is referable to one of the smaller species of *Ondatra*, such as *O. idahoensis*.

The Curtis and Benson mammalian assemblages, exclusive of the rodents, suggest a difference in age. However, both faunas seem to come from approximately the same stratigraphic horizon, in the same formation. While the rodent faunas do not suggest any great difference in age, few species are found to be common to both.

The problem of the San Pedro Valley faunas is also confused by a somewhat anomalous association of Pliocene and Pleistocene types among the larger mammals. The apparent association of *Lepus* with some of the more primitive types of larger mammals is also confusing. The problem of these faunas will be discussed in more detail elsewhere.

PLIOCENE RODENT EVOLUTION

FAMILY ISCHYROMYIDÆ

The Ischyromyidæ have not been recorded from the Pliocene. Their last appearance may have been in the John Day faunas. *Kansasimys* Wood (1936b), a genus of uncertain affinities, may be related to the ischyromyids, but the probability is not very great. Comments on this rodent type have been made in an earlier section of the present paper. It might be added that A. E. Wood has compared this genus on the one hand with the cylindrodonts and the ischyromyids (*s.s.*), and on the other with *Sciuravus*.

FAMILY MYLAGAULIDÆ

This family of fossorial rodents seems to become extinct by the end of the middle Pliocene. It has not been certainly recorded from any upper Pliocene beds.

The evolution of the family is not well known. Even the important question of individual and age variation has not been solved. There are probably two distinct phyla, one horned, the other hornless. The alternative view that the presence of horns is a sex character seems less likely; the absence of horns would place the female at a considerable disadvantage, since the horns apparently were used in digging. Moreover, there seems to be a preponderance of hornless types. Of the several skulls in the California Institute collections, none exhibits horns.

Horned mylagaulid types may not occur above the lower Pliocene. Of the two specimens with horns which have been described, *Ceratogaulus* is from the Pawnee Creek beds, and *Epigaulus* from the Republican River. Gidley in his original description of the latter genus

referred the beds from which it came to the upper Miocene. However, the Republican River is usually considered as of lower Pliocene age. Since the beds are generally placed as slightly younger than the

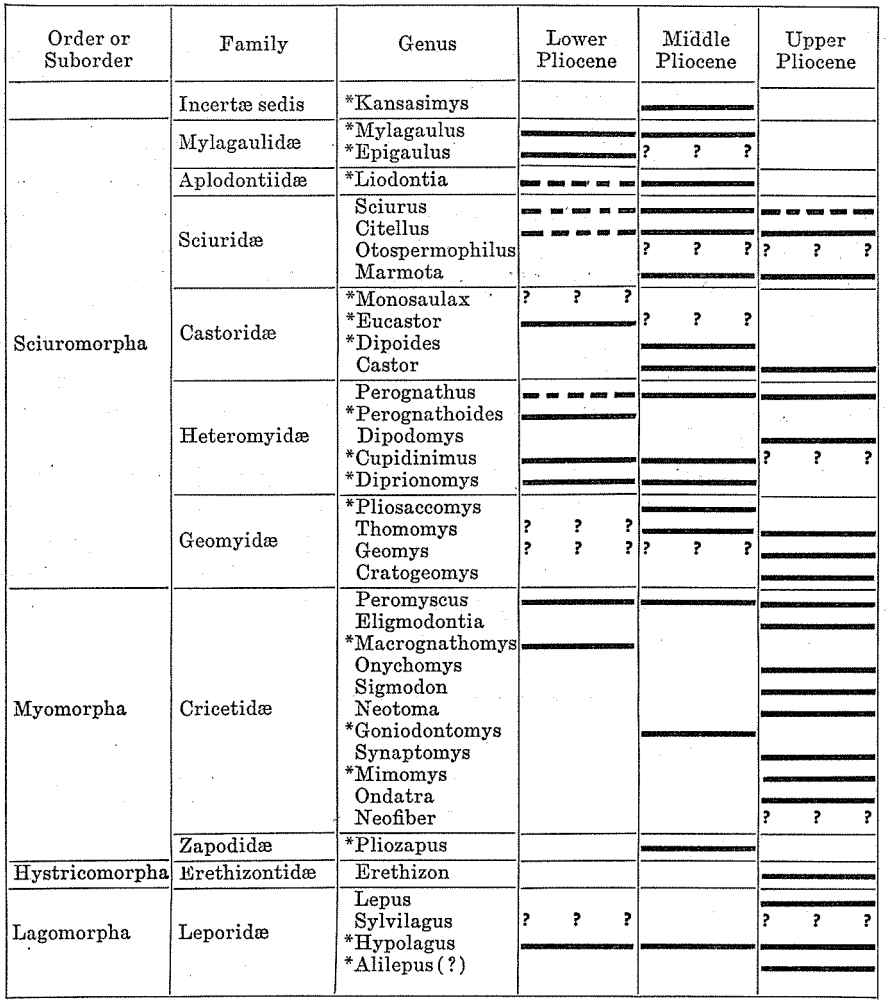

FIG. 1—Distribution of Pliocene rodent and lagomorph genera

Present.

Undoubtedly present but not recorded (present both before and after a particular stage).

? ? ? Questionably present for one or more of the following reasons: (1) taxonomic position doubtful; (2) stratigraphic position doubtful; (3) age of beds doubtful.

* Extinct.

Valentine, their age is practically equivalent to that of some of the formations referred to the middle Pliocene in this paper. Moreover,

it has been suggested that the Republican River is in part composite (see Simpson, 1933, p. 107) and that the *Epigaulus* locality (Long Island quarry) is of later age than that usually assigned to the formation, and hence typically middle Pliocene (Teilhard and Stirton, 1934, p. 284, table 3).

Two species of mylagaulids have been definitely recognized in the Pliocene, namely, *Mylagaulus monodon* and *M. sesquipedalis.* The types of both species are, however, from beds of questionable age. The two are distinguished by the fact that *M. sesquipedalis* is smaller, possesses fewer lakes, the lakes are less elongate, and more irregularly arranged. *M. monodon* is the more common type and practically all Pliocene mylagaulids have been referred to this species. It differs from the more distinctive Miocene forms by its large size, relatively large number of lakes, tendency of lakes to align themselves in rows, and by the fact that cement frequently forms an integral part of the wearing surface of the teeth (as in *Mesogaulus*). According to Matthew, the type of *M. monodon* is probably identical with *Epigaulus hatcheri.*

It is not practical to discuss here more fully the problems associated with the Mylagaulidæ. In many ways little is known about the group, and present knowledge has been summed up by various authors, principally by Matthew (1924). More specific discussion of a few of the problems has been presented in a paper dealing with the Rome, Oregon, rodent fauna (Wilson, 1937).

FAMILY APLODONTIIDÆ

The known history of the Aplodontiidæ extends from the upper Eocene to the Recent. However, aplodontids are relatively rare as fossils, and the post-John Day forms are limited to the middle Miocene *Liodontia,* middle Pliocene *Liodontia,* Pleistocene and Recent *Aplodontia,* and a single species from Asia, *Pseudaplodon asiatica* (lower Pliocene?).[1] In addition, a single upper premolar of an aplodontid is known from the Cedar Mountain region. Stirton (1932) has made the most recent determination on this specimen and regards it as representing *Meniscomys,* and as middle Miocene in age. It is more probable, however, that the specimen represents a Dp4 of *Liodontia alexandræ* or closely related species, as suggested by C. L. Gazin (1932, p. 67), unless Stirton has obtained additional material from this locality.

The chief changes which took place between the middle Miocene and middle Pliocene were, in Pliocene forms: (1) mesostyles on upper teeth more acute, (2) reduction of ventral protuberance on lower

[1] For a discussion of the relationships of this form, see the remarks at the end of this section.

jaws (approaching *Aplodontia*), (3) changes in development and position of masseter muscle (strongly developed and slightly farther forward, approaching *Aplodontia*), and (4) antero-external fold of lower molars more reduced. There was apparently no increase in size. (Gazin, 1932, pp. 63–67.)

Liodontia is usually assigned to a position intermediate between *Meniscomys hippodus* and the Quaternary *Aplodontia.* The later Tertiary form is distinguished from *Aplodontia* by the absence of a mesostylid on the lower molars of the former genus, and by an early reduction of the antero-external fold in the lower cheek-teeth. While *Liodontia* is certainly intermediate between the John Day and Recent aplodontids, it seems rather doubtful to the author that *Aplodontia* is a direct descendant of the Tertiary genus.

Remarks on the Asiatic Rodent *Pseudaplodon asiatica* (Schlosser)

Max Schlosser in 1924 described what he believed to be an authentic record of a Tertiary (lower Pliocene?) aplodontid from Mongolia. The material, consisting chiefly of a lower jaw with dentition, was described as *Aplodontia asiatica,* new species. Later, Miller (1927) expressed doubt as to the affinity of this form with the aplodontids, suggesting that the animal represented a member of the dipodine group. At the same time, he erected the genus *Pseudaplodon* for the Asiatic form. Lastly, Gazin (1932) in his report on the Skull Spring mammalia of southeastern Oregon compared specimens of *Liodontia alexandræ* with Schlosser's species and suggested that the latter had separated from the aplodontid stock at a time when the development had reached a stage between *Meniscomys hippodus* and *L. alexandræ.* Gazin apparently did not doubt the aplodontid affinities of the Mongolian material, nor did he make any reference to Miller's views. However, he changed the original determination to *Aplodontia*(?) *asiatica.*

Perhaps a discussion of the affinities of *Aplodontia asiatica* lies beyond the scope of this paper, but the occurrence of an aplodontid in Mongolia, if substantiated, is of sufficient interest to justify a statement at this point. The taxonomic position of fragmentary rodent material, as Miller pointed out, is often extremely difficult to determine. In the present case even the scanty material is not at hand and only the original figures are available. It should be pointed out that Dr. Miller was aided in arriving at his conclusions by an examination of photographs which revealed some characters not clearly made out, or seen at all, in the published figures.

In support of his argument that *A. asiatica* is not related to the aplodontids, Miller presents the following points based on characters in the Asiatic species:

1. No mesostyle on cheek-teeth, whereas this is a fundamentally important structure in the aplodontids.

2. Small enamel lake near middle of crown in $P\overline{4}$, $M\overline{2}$, and $M\overline{3}$, obviously the last remnant of an infolding of enamel from the inner side of the crown. Such a re-entrant fold does not occur in *Aplodontia* at any age.

3. Presence of a broad, well-developed re-entrant angle on the anterior margin of crown of $P\overline{4}$, a region which in *Aplodontia* presents a smoothly rounded, forwardly directed convexity.

4. Anterior border of ascending ramus extends almost straight backward, and remains below the level of alveolar border to point where it is broken off, whereas in *Aplodontia* the anterior border of the ascending ramus curves up abruptly, high above the tooth-row from about the level of the second molar.

5. Part of jaw lying below the premolar is not deepened in the manner which is characteristic of *Aplodontia*.

6. Mandible shows a well-defined basin-like depression in the region between the hinder termination of the incisor (which is at level of space between $M\overline{2}$ and $M\overline{3}$, as in *Aplodontia*) and the base of the angular process. No such depression exists in *Aplodontia*.

7. Form of angular process is obviously different from that in the American animal, but neither the drawing nor the photographs represents this part of the jaw with adequate clearness.

With reference to the cheek-tooth characters stated by Miller, the following comments may be made from a study of the material from Skull Spring representing *Liodontia alexandræ*:

1. The mesostyle is indeed well developed in the aplodontids, but the corresponding structure in the lower grinders is absent in *Liodontia*.

2. Enamel lakes are present in the lower premolars of *L. alexandræ* until an advanced stage of wear. Two specimens of this species from Skull Spring exhibit lakes in $M\overline{3}$; another indicates the possible presence of a lake in $M\overline{1}$. Moreover, a study of John Day aplodontids shows that the presence of lakes certainly does not prohibit *A. asiatica* from having affinities with these animals.

3. A re-entrant angle at the anterior margin of $P\overline{4}$ is present at an early stage of wear in *L. alexandræ*.

Thus it seems that so far as dental pattern is concerned, there is apparently no valid reason for excluding the Mongolian species from the aplodontids. Comparison of characters in the ramus of *A. asiatica* with those of *Aplodontia* and *Liodontia* is difficult on the basis of Schlosser's figure and the material representing *Liodontia* which I have at hand. So far as the figure of *A. asiatica* is concerned, the ramus of that animal is not strikingly different from the corresponding

part in *Liodontia,* at least with regard to group separation. However, the photographs available to Miller show apparently major differences which prevent assignment of *A. asiatica* to any American aplodontid. Hence, the following comments involve considerably less valid objections to Dr. Miller's views than those on the dental characters.

4. If Miller is right in interpreting his photographs to mean that this character is not due to breakage of the jaw, it is a major difference separating the Asiatic form from either *Liodontia* or *Aplodontia.* However, most of the Skull Spring specimens are broken in this region, and this may be a rather common area of breakage. On this point difficulty may be encountered in an interpretation of even very clear photographs.

5. The deepening of the ramus below $P\overline{4}$ is not strikingly different from that in *L. alexandræ,* although the Skull Spring form may possess a slightly deeper jaw.

6. No remarks.

7. As far as Schlosser's figure is concerned, the angle is not very different from that in *Liodontia* and hardly seems to be of family importance, although Miller's photographs may show pronounced differences.

Conclusions—The dental characters stressed by Miller as separating *Aplodontia asiatica* from the aplodontids do not appear to be valid. Characters of the ramus seemingly prohibit an assignment of the species to any known genus of aplodontids. Although these characters may also exclude *A. asiatica* from relationship with the aplodontids, the agreement in dental pattern is such as to suggest this relationship rather than one with dipodine forms. In the latter group of rodents, so far as I know, there are no types which have dental patterns similar to that of *A. asiatica* and which also possess large lower premolars. In view of the geographic position of *A. asiatica,* its probable geologic age, and the character of the dental pattern, which Gazin has suggested is intermediate between *Meniscomys* and *Liodontia,* the generic name proposed by Miller is apparently valid. The Mongolian species is consequently designated as *Pseudaplodon asiatica* (Schlosser), and assigned to the Aplodontiidæ as that family is defined in this paper.

FAMILY SCIURIDÆ

The Miocene has furnished more or less complete skulls of both *Sciurus* (tree-squirrel) and *Citellus* (ground-squirrel). The forms, as for example those recorded in the Skull Spring middle Miocene fauna, probably do not represent Recent *Sciurus* and *Citellus* in a strict sense. In a broad way, however, they do typify a differentiation into tree-squirrel and ground-squirrel groups.

No skulls or even fragments of skulls have been secured as yet from Pliocene beds. Hence our entire knowledge of the family for the Pliocene epoch is based on the dentition. Unfortunately, the dentition is extremely stable in the Sciuridæ. It is the little-modified descendant of the ancestral *Paramys* type, and in this respect is closer to the ancestral stock of the Rodentia than that of any other modern family of rodents. As a result, Pliocene sciurids offer little help in problems of correlation. Tree-squirrels and intermediate types of ground-squirrels that are fairly close to Recent forms are found in Pliocene strata. Some of the more specialized sciurids, such as *Marmota*, are also recorded. Noteworthy perhaps is the fact that no typical ground-squirrel of the genus *Citellus* has been recorded so far in strata older than the upper Pliocene. Hence the first appearance of these sciurids may be of value in correlation. However, until more complete phylogenies of the Sciuridæ are established, this fact is negative evidence and should be used with caution.

FAMILY CASTORIDÆ

Pliocene beavers appear to be represented only by the genera *Eucastor*, *Dipoides*, and *Castor*. These genera fall into two distinct phyla. Pliocene *Castor* represents the more primitive ancestor of the existing beaver (*Castor*), and *Eucastor-Dipoides* culminates perhaps in the Pleistocene giant beaver, *Castoroides*.

The earliest appearance of *Castor* on this continent may be in the upper Snake Creek and Rome middle Pliocene faunas. Members of the genus are not abundant, however, until the upper Pliocene. Pliocene *Castor* possesses distinctly shorter-crowned teeth than do Quaternary representatives of the genus, and with more complete material it may be found necessary to distinguish the former, at least in part, under a separate generic name. Somewhat similar forms in the Pliocene of Asia have been included in a distinct genus, *Sinocastor*, by Young. The direct ancestor of *Castor* is not found in North America, and Pliocene forms on this continent probably migrated here during this period. However, the lower Miocene *Palæocastor* is perhaps ancestral in a broad way to the line terminating in *Castor*.

Eucastor and *Dipoides* are successive types of an evolutionary series beginning with *Monosaulax* of the middle and upper Miocene and possibly leading to *Castoroides*. *Dipoides* is restricted apparently to the middle Pliocene in North America. *Eucastor* is characteristic of the lower Pliocene, although it is recorded also from the upper Snake Creek. Its presence in the middle Pliocene fauna may be the result of a reworking of the material evidence or of a mixing of specimens during collecting. An alternate explanation is that it is a survivor from the lower Pliocene.

Dipoides is distinguished from *Eucastor* by (1) a lengthening of the tooth-crown, (2) simplification of cheek-tooth pattern, and persistency of the simplified pattern (*i.e.*, resistance to the formation of lakes), and (3) larger size.

Possibly, as has been mentioned above, *Dipoides* in turn gave rise to *Castoroides*, since otherwise the Pleistocene genus stands in a strangely isolated position. This view has been advocated by Matthew, and more recently by Stirton. In support of this belief is the striking resemblance in cheek-tooth pattern, and continued increase in hypsodonty and size. However, *Castoroides* has been placed in a distinct family, the Castoroididæ, by Hay, Gidley, and others, on the basis of the quite noticeably modified skull. A skull of *Dipoides* described by Young (1927) appears to be fairly close to *Castor*. It might be added that although *Castoroides* shows an increase in size over *Dipoides*, this increase is tremendous. It is curious, therefore, that a beaver phylum in which the various species have been smaller than other castorids during most of its evolutionary history should suddenly give rise to the largest of all known beavers and the largest rodents of North America. Unfortunately, no upper Pliocene types are known which are related to either *Dipoides* or *Castoroides*, so that the descent of *Castoroides* cannot be definitely determined. Perhaps the fact that in some individuals of *Dipoides stirtoni* the fourth upper premolar possesses antero-external and internal inflections which are confluent, cutting through the narrow isthmus of dentine present in the more normal tooth (Wilson, 1934, pl. 1, fig. 4), foreshadows the character of the cheek-teeth in *Castoroides*.

Beaver types are known from the Valentine fauna (upper Miocene or Miocene-Pliocene?) which are intermediate between *Eucastor* and the Miocene *Monosaulax*. Typical *Monosaulax*, however, is less progressive than *Eucastor* with less hypsodonty in the cheek-teeth and more tendency to form isolated lakes. Until Stirton's work on the Tertiary beavers, *Monosaulax* was confused with *Palæocastor*, but the genus apparently is more closely related to the Old World *Steneofiber* than to North American palæocastors.

FAMILY HETEROMYIDÆ

All three Recent subfamilies of Heteromyidæ were in existence by lower Pliocene, namely the Perognathinæ (pocket-mice), Dipodomyinæ (kangaroo-rats), and Heteromyinæ (spiny pocket-mice). Representatives of the kangaroo-rats were not very clearly differentiated at this time, however, a fact which perhaps indicates that this group is not so important as a division of the family as are the other two. The only Recent genus of heteromyid in existence by the lower Plio-

cene is *Perognathus*, the most unspecialized of the modern genera in regard to dentition.

In contrast, during the upper Pliocene the only extinct genus so far recorded is *Cupidinimus*. Even the presence of this genus in the upper Pliocene is doubtful, although the form represented is not referable to any living genus.

Several aberrant lines are indicated by Pliocene heteromyid material. *Cupidinimus magnus* appears to be an aberrant kangaroo-rat, *Perognathoides* an aberrant pocket-mouse, and *Diprionomys* an aberrant heteromyine. Unfortunately, as is so often the case with fossil rodents, as well as larger mammals, only the approximate ancestors of Recent genera are known. Exception to this statement is seen in the Pliocene *Perognathus*, and possibly a genus (undescribed) from the Valentine fauna which is related to the Recent *Microdipodops*. The direct ancestors of the living spiny pocket-mice, *Heteromys* and *Liomys*, are not known.

The detailed evolution of the Heteromyidæ is too involved for discussion in the present paper. For further particulars, A. E. Wood's paper on the Heteromyidæ should be consulted (Wood, 1935).

Pliocene heteromyids are represented by the following genera:

Lower Pliocene
**Cupidinimus, *Perognathoides, *Diprionomys, Perognathus*
Middle Pliocene
**Cupidinimus, *Diprionomys, Perognathus*
Upper Pliocene
*?*Cupidinimus, Dipodomys, Perognathus*

* Genus extinct.

FAMILY GEOMYIDÆ

In spite of some determinations to the contrary, Pliocene gophers appear to be restricted to the group of true gophers of the subfamily Geomyinæ. The extinct group of the Entoptychinæ has been reported from the Pliocene in two occurrences. A single tooth from the Fish Lake Valley beds was referred by E. Raymond Hall to *Entoptychus?*. However, Hall pointed out that reference of the specimen to the Geomyidæ is doubtful, and, as has been mentioned, A. E. Wood has suggested that the specimen represents a lagomorph. Miss Louise Kellogg referred a specimen from the Thousand Creek to *Entoptychus minimus* new species. This species is congeneric with *Diprionomys* from the same locality, and perhaps specifically identical with *D. parvus*. In other words, it is a heteromyid and not a geomyid.

Lower and middle Pliocene gophers are in a state of considerable confusion. Some of these, as for example *Pliosaccomys*, are far removed from Recent genera. The Recent forms, *Geomys* and

Thomomys, have been reported from the early Pliocene and even from the Miocene. It must be admitted that it seems quite likely that *Thomomys,* at least, was present by lower Pliocene time. On the other hand, no adequate description of any gopher material referable to a Recent genus and occurring in the lower and middle Pliocene has ever been published. Not a single specimen has been figured.

The first undoubted Recent genera are from the upper Pliocene, and *Geomys, Cratogeomys,* and *Thomomys* have been reported from this stage.

The genus *Pliosaccomys* from the early Pliocene appears to be a true geomyid, although a very primitive form for so late a stage in time. It is highly probable that this genus is aberrant, certainly so if *Thomomys* is actually present in the lower Pliocene. However, in the absence of any other types which are adequately known, it may be employed to suggest at least the main features of Pliocene evolution among gophers. The relationships of this form are discussed in a paper by the author on the Smiths Valley rodent fauna (Wilson, 1936).

Characters in *Pliosaccomys* together with certain features of the Recent genera, especially the character of unworn geomyid teeth, suggest that evolution in the Pliocene or at least the later Tertiary proceeded toward acquiring (a) persistent growth of crown, (b) differentiation of the enamel of the tooth-crown into discontinuous bands, and (c) more completely fossorial characters.

FAMILY CRICETIDÆ

The evolution of later Tertiary cricetids is very poorly known even for rodents. Only three genera have been recognized in the lower and middle Pliocene, and only one of these, the Recent genus *Peromyscus,* has any descendants in the upper Pliocene and Quaternary. Hence, observations on the evolution of the family during the Pliocene are limited to remarks on *Peromyscus* and a few statements concerning the relations of upper Pliocene cricetid species to Recent species.

The family Cricetidæ may be conveniently divided into two groups, the Cricetinæ and the Microtinæ. The former group is characterized by rooted molars whose crowns are normally brachydont and tubercular. There is a gradual transition to more flat-topped, prismatic teeth. The teeth are never rootless, however, and the posterior terminations of M1 and M2 are never angular. This group comprises the forms usually referred to as rats and mice (deer-mice, cotton-rats, wood-rats, and so forth). The Microtinæ are characterized by possessing flat-topped, prismatic teeth, which are usually but not in-

variably rootless. The posterior terminations of M1 and M2 are angular. They are the voles and lemmings.

CRICETINÆ

Two genera of cricetines are known from the lower Pliocene, the Recent genus *Peromyscus* and *Macrognathomys*. The latter form is apparently aberrant and need not be considered further. *Peromyscus* is represented by a single species from Fish Lake Valley, *P. dentalis*. Compared with Recent species, it is characterized by low-crowned teeth and relatively unreduced third lower molars. It is much smaller than middle Pliocene members of the genus.

Peromyscus is the sole cricetine genus known from the middle Pliocene. Two species are present. Both differ from the lower Pliocene form in much larger size and higher-crowned teeth. They approach *P. dentalis* in possessing a relatively unreduced $M\overline{3}$, and thus differ from upper Pliocene and Quaternary species, in which $M\overline{3}$ is usually more reduced. The difference in size between lower and middle Pliocene forms is perhaps made more convincing by the fact that *Peromyscus* or *Peromyscus*-like species from the upper Miocene of the Barstow and Tonopah faunas are also much smaller than middle Pliocene forms. Thus it seems possible that the middle Pliocene was characterized by the existence of "gigantic" representatives of *Peromyscus*. The statement, of course, is not meant to imply that large types were the sole representatives of *Peromyscus* or *Peromyscus*-like forms at this stage, nor even that small forms only were present in the older or younger phases of the Pliocene. However, the known size distribution in time is suggestive, as is the fact that extremely large species of *Peromyscus* are now confined to quite southern regions.

In a strict sense, the genus *Peromyscus* probably does not exist previous to the upper Pliocene, and the earlier species should receive separate generic recognition. However, in view of the present state of our knowledge it is perhaps best to continue to refer these related types to *Peromyscus*.

The known upper Pliocene species of *Peromyscus* are relatively small forms with reduced third lower molars.

Upper Pliocene cricetines, in contrast to the preceding stages, are known by a number of rather diverse genera, all of which are still living. It is worth noting, however, that although the genera are living, the species are extinct.

Unfortunately, all of our upper Pliocene cricetines come from the Benson and Curtis faunas of the San Pedro Valley. Thus, not only do we know nothing of the upper Pliocene cricetines of other parts of

western North America, but the nature of the San Pedro Valley occurrence introduces doubt as to the exact age of the fauna from this area. In these assemblages we find the earliest record of *Sigmodon* (cotton-rat), *Onychomys* (grasshopper-mouse), and *Neotoma* (wood-rat). Moreover, *Eligmodontia* is likewise recorded from this locality. This genus is of interest since it is now limited to South America. Whether the Arizonan species was invading or leaving North America at that time is not known. It is not necessary to discuss the detailed characters which separate the upper Pliocene cricetines from their living relatives. The characters are minor ones but apparently distinct.

Microtinæ

Pliocene microtines are practically confined to the upper stage of the epoch. This statement has world-wide application at present. The earliest record of a microtine may be that of *Poamys* from the lower Snake Creek Miocene. Matthew has suggested that the genus is a structural ancestor. The genetic relationship of this genus to the microtines remains to be proved. The only other pre-upper Pliocene record is that of the genus *Goniodontomys* occurring in the Rome fauna of middle Pliocene age. Reference of this genus to the microtines is perhaps open to some doubt, but it seems closer to this group than to any other. *Goniodontomys,* if a vole, is an aberrant member of the group without descendants.

Certain upper Pliocene localities have yielded abundant, if incomplete, remains of Microtinæ. They are markedly less advanced than Recent types. In most of them, in comparison with Recent forms, there is a decided difference in tooth-pattern, less persistent growth of the cheek-teeth, and a lack of cement deposit on the teeth. Some upper Pliocene microtines are even distinct generically from Recent types. Both voles and lemmings are represented in the faunas. The latter are the only myomorphs with rootless teeth so far discovered in the North American Pliocene.

The microtine group has been used in Europe with marked success in correlation problems. Work on this group in North America also should prove valuable. These rodents may even furnish a means of zoning our upper Pliocene–Pleistocene, certainly a difficult task with most other groups of mammals. The Microtinæ also offer possibilities of intercontinental correlation, especially with regard to the genus *Mimomys.*

The following cricetids have been recorded from the Pliocene:

Lower Pliocene
*Peromyscus, *Macrognathomys*
Middle Pliocene
*Peromyscus, *Goniodontomys*
Upper Pliocene
*Onychomys, Sigmodon, Peromyscus, Eligmodontia, Neotoma, ?Neofiber, Synaptomys, Ondatra, *Mimomys*
* Genus extinct.

It is evident from the above list that few of the upper Pliocene genera have any known ancestors in the earlier Pliocene. This point will be discussed later in some detail, as it has an important bearing on correlation of rodent faunas.

FAMILY ZAPODIDÆ

The only known North American Tertiary representative of the Zapodidæ is *Pliozapus* from the middle Pliocene of Smiths Valley, Nevada. Strangely enough at first sight, this genus is more closely related to the Recent Asiatic genus *Eozapus* than it is to either *Zapus* or *Napæozapus,* Quaternary representatives of the family on this continent. In cheek-tooth characters *Eozapus* is distinctly more primitive than either *Zapus* or *Napæozapus,* which explains to some degree its closer approximation to *Pliozapus. Pliozapus,* as represented by its single species *solus,* could hardly have given rise to *Eozapus,* as the species seems already too specialized. However, in most of its characters it is a good structural ancestor to the Asiatic type. If the Smiths Valley genus is ancestral also to Recent North American types, considerable evolution must have taken place in height of crown and more particularly in the development of the highly complex tooth-patterns of *Zapus* and *Napæozapus.* The ramus of *Pliozapus,* however, is quite close to that of Recent North American zapodids.

The North American ancestors of *Pliozapus,* if they are to be found on this continent, are quite unknown unless the Sespe Eocene *Simimys* proves to be a zapodid. *Protoptychus* from the Uinta and *Paciculus* from the John Day have both been referred by Hay to the Dipodoidea. A. E. Wood has suggested recently that *Paciculus* is a cricetid.[1] *Protoptychus* even if a dipodid cannot be more than distantly related to *Pliozapus.* Moreover, both *Protoptychus* and *Simimys* are so far removed in time from *Pliozapus* that, whatever their true relationships, they can have little real bearing on the problem of later zapodid evolution.

FAMILY ERETHIZONTIDÆ

Hystricomorphs are typically developed in South America, and all North American forms are invaders from that continent, or descend-

[1] A. E. Wood, Amer. Mus. Nov., No. 822, 4–5, 1936.

ants of those invaders. For this reason, no hystricomorphs are found in North America before the establishment of the later Tertiary union with the southern continent.

The first undoubted appearance of the group in North America is seen in the presence of the extinct species *Erethizon bathygnathum* in the upper Pliocene Grand View fauna. The principal differences between this species and living North American porcupines are in the heavier jaw and slightly different tooth proportions.

The first appearance of hystricomorphs on this continent should furnish an important marker when the date is definitely established. South American sloths have been found in our faunas as early as the upper Snake Creek and Rattlesnake, so that it is not certain that the upper Pliocene marks the first appearance of southern rodents in North America. Moreover, *Hystricops* Leidy (upper Miocene?) has been referred at various times to the beavers and to the porcupines. Stirton considers this genus a castorid.

FAMILY CAVIIDÆ

Types related to the living giant capybara of South America are found in the Pleistocene faunas of North America. So far, none of these forms has been recorded from the Pliocene.

FAMILY OCHOTONIDÆ

As has been mentioned previously, the lagomorphs are not rodents in a strict sense. Since, however, the order Lagomorpha is so restricted and compact, and since it is usually associated with rodents in a popular sense, both groups are included in the present paper.

The lagomorph family Ochotonidæ or pikas have not been definitely recorded in the Pliocene. The presence of an aberrant ochotonid in the Virgin Valley middle Miocene fauna and the occurrence of *Ochotona* in the Recent fauna implies their presence in the Pliocene. Perhaps undescribed pikas are in existence in Pliocene lagomorph collections but have been confused with leporids.

FAMILY LEPORIDÆ

No definitely observable evolutionary changes take place in Pliocene Leporidæ. The genera include **Hypolagus, Sylvilagus?,* **Alilepus?, Lepus,* and *Sylvilagus* or *Brachylagus. Hypolagus* is the most important Pliocene genus, and *Lepus* deserves mention because of stratigraphic problems attached to its first appearance in North America. The remaining genera are of minor importance and will not be mentioned further.

The generic status of *Hypolagus* has long been a subject of considerable debate. Matthew always held to the view that there was not

sufficient evidence to warrant its recognition as a distinct genus. However, later work with additional material and the general tenor of the evidence suggest that *Hypolagus* is entitled to generic rank. Moreover, distinct or not in a strict taxonomic sense, the genus is distinguishable from *Lepus,* and there is little evidence to indicate that it ever gave rise to the Recent *Lepus.*

Hypolagus and *Lepus* have never been found in association in the Pliocene of North America, and the only fauna in which this occurs is the lower(?) Pleistocene Anita, Arizona, assemblage. In this case the species of *Hypolagus* present in the fauna may not be a typical *Hypolagus.* This is the last appearance of the genus.[1] The earliest record of *Lepus* in North America is in the Benson and Curtis faunas of San Pedro Valley, Arizona.

The present author regards true *Lepus* as probably an emigrant from Asia and believes that its appearance in North America brought about a rapid extinction of *Hypolagus.* Dr. Dice (1929, pp. 343–344) appears to have indirectly suggested this same view. Moreover, if this is true, *Lepus* seems to have arrived at about the opening of the Pleistocene as defined in this paper, and faunas in which *Hypolagus* but not *Lepus* is present are older than faunas in which the modern genus is a member. According to this view, the Grand View and Hagerman faunas are older than the San Pedro Valley faunas, if *Lepus* is actually a member of these assemblages. Since the statement that the San Pedro Valley assemblages are younger than those from Grand View and Hagerman is probably not countenanced by many or any American palæontologists at present, a fuller discussion will be presented in a later section of this paper.

ANALYSIS OF PLIOCENE RODENT FAUNAS

The following lists are in part a repetition of those already given. They are repeated for the sake of clearness in the presentation of the following sections. Most of the doubtful genera have been omitted. Likewise genera which are undoubtedly present (for example *Liodontia* in the lower Pliocene), but have not been definitely recorded, are also omitted. The latter omission is made in order to give ratios of sciuromorphs to myomorphs without including genera that have not actually been found. Disposition of the Valentine fauna and of

[1] L. R. Dice has referred *Lepus giganteus* Brown from the Conard Fissure to *Hypolagus.* The type and only known specimen is a fragment of skull with P3 and P4. Recently C. Bertrand Schultz has referred a lagomorph jaw from the middle(?) Pleistocene of Nebraska to this species, retaining the original generic designation (Nebr. State Mus., vol. 1, bull. 41, 1934). The type specimen hardly seems adequate for definite assignment to *Hypolagus.* Apparently Dice based his determination on the fact that in *L. giganteus* the enamel re-entrants of the cheek-teeth extend only slightly more than halfway across the occlusal surface. In *Lepus* these re-entrants extend about three-quarters of the distance across the tooth.

other assemblages in which the age of the forms is doubtful has been somewhat arbitrary. For instance, *Cupidinimus nebraskensis* has been omitted because of possible Miocene age. Balancing this omission to a certain extent is the inclusion of *Diprionomys* on the evidence of its presence in the Devil's Gulch beds. In view of the uncertain systematic position of *Kansasimys*, this genus has been excluded from consideration.

LOWER PLIOCENE

Order Rodentia
- *Family Ischyromyidæ
  - None
- Family Aplodontiidæ (North America and Asia)
  - None recorded
- *Family Mylagaulidæ (North America)
  - **Mylagaulus*
  - **Epigaulus*
- Family Sciuridæ (practically world-wide distribution)
  - None recorded
- Family Castoridæ (Northern Hemisphere)
  - **Eucastor*
- Family Heteromyidæ (North and Central America; northern part of South America)
  - **Perognathoides*
  - **Diprionomys*
- Family Geomyidæ (North and Central America)
  - None recorded?
- Family Cricetidæ (practically world-wide distribution)
  - *Peromyscus*
  - **Macrognathomys*
- Family Zapodidæ (North America and Eurasia)
  - None
- Family Erethizontidæ (North and South America)
  - None
- Family Caviidæ (South America; Pleistocene of North America)
  - None

Order Lagomorpha
- Family Ochotonidæ (Holarctica)
  - None recorded
- Family Leporidæ (practically world-wide distribution)
  - **Hypolagus*

* Genus extinct.

Lower Pliocene extinct genera	7
Lower Pliocene living genera	1
Lower Pliocene sciuromorph genera	5
Lower Pliocene myomorph genera	2
Lower Pliocene hystricomorph genera	0

If lower Pliocene genera that are known to be present but have not been recorded so far are added to the above list, the predominance

of sciuromorphs over myomorphs is increased to five to one. The number of types is not sufficiently large to permit this ratio to mean much in a numerical sense, but it is nevertheless true that the sciuromorphs greatly outnumber the myomorphs. Practically all known lower Pliocene rodents represent extinct genera. Even *Peromyscus*, in the above list, is probably generically distinct from the living form. The only living North American genera which very likely extend back without generic change to the lower Pliocene are *Perognathus, Sciurus, Citellus* (in the broad sense), and possibly *Thomomys*.

It should be noted that there is no decided faunal break between the upper Miocene and lower Pliocene faunas. None of the lower Pliocene genera appears to be an introduced type, and the entire fauna evolved from existing North American Miocene forms. Probably the only very distinctive rodent type for this stage is *Eucastor*.

The lower Pliocene rodent faunas may be characterized as follows:

1. Great preponderance of sciuromorphs over myomorphs.
2. High percentage of extinct genera.
3. No strikingly new or introduced types.
4. Presence of the genus *Eucastor*.

MIDDLE PLIOCENE

Rodentia
- *Family Ischyromyidæ
  - None
- Family Aplodontiidæ
  - **Liodontia*
- *Family Mylagaulidæ
  - **Mylagaulus*
- Family Sciuridæ
  - *Sciurus*
  - *Citellus*
  - *Marmota*
- Family Castoridæ
  - **Dipoides*
  - *Castor*
- Family Heteromyidæ
  - **Diprionomys*
  - **Cupidinimus*
  - *Perognathus*
- Family Geomyidæ
  - **Pliosaccomys*
  - *Thomomys*
- Family Cricetidæ
  - **Goniodontomys*
  - *Peromyscus*
- Family Zapodidæ
  - **Pliozapus*
- Family Erethizontidæ
  - None
- Family Caviidæ
  - None

Lagomorpha
- Family Ochotonidæ
  - None recorded
- Family Leporidæ
  - **Hypolagus*

* Genus extinct.

Middle Pliocene extinct genera	9
Middle Pliocene living genera	7
Middle Pliocene sciuromorph genera	12
Middle Pliocene myomorph genera	3
Middle Pliocene hystricomorph genera	0

Because of the large number of known middle Pliocene genera, the sciuromorph preponderance over the myomorphs is more striking.

There are relatively fewer extinct genera. The ratio of living to extinct genera during this stage is about one to one. Several introduced or at least distinctly new types are present, namely, *Castor, Goniodontomys*, and possibly *Pliozapus*. The introduction of the true beaver phylum (*Castor*) from the Old World is fairly well established. Moreover, the only beavers that appear to be related to *Castor* and are older than middle Pliocene are Old World types. The microtine genus *Goniodontomys* may also have an Old World background. It is usually agreed upon that the Old World was the seat of higher myomorph evolution, but it should be pointed out that no microtine older than, or as old as, *Goniodontomys* has ever been found there. If *Poamys* from the lower Snake Creek can be shown to be approximately ancestral to the Microtinæ, this continent may after all be the site of evolution of some of the higher Myomorpha. *Pliozapus* may also be an introduced type, but it seems possible that North America was the place of evolution of the Zapodinæ. The most distinctive middle Pliocene rodent is the beaver genus *Dipoides*. *Dipoides* appears to be characteristic for the mid-Pliocene everywhere in North America. It should be noted that the Mylagaulidæ become extinct with the close of this stage. It has already been pointed out that large species of *Peromyscus* are characteristic of the middle Pliocene.

Middle Pliocene rodent faunas may be characterized as follows:

1. Great preponderance of sciuromorphs over myomorphs.
2. Approximately equal number of extinct and living genera represented.
3. Introduction of *Castor* in later faunas.
4. First appearance of Microtinæ.
5. Presence of "gigantic" *Peromyscus*.
6. Presence of the genus *Dipoides*.
7. Last appearance of the mylagaulid rodents.

So far nothing has been said concerning conclusions which may be drawn with reference to the ecologic conditions under which the various faunas lived, and which prevailed in general during the lower and middle Pliocene. Most of our rodent faunas are too incomplete to draw any very definite conclusions. Moreover, although we know a great deal about the ecology of living rodents, the application of this knowledge to fossil forms becomes increasingly uncertain as we go back in geologic time. In all probability forms which at present are restricted to certain types of environment enjoyed a wider field in the past. In addition, many genera of living rodents occupy a wide range of environments even though particular species or races are sharply restricted. Hence the presence of a related type in the Pliocene does not often suggest definite living conditions. However, in many Pliocene rodents there is an increase in hypsodonty in middle Pliocene

forms over those of the lower. The suggestion may be made that this is in response to the increasing aridity which occurred with the passing of Pliocene time, a response which culminated in the upper Pliocene in the appearance of many of our Recent genera with long-crowned teeth.

UPPER PLIOCENE

Rodentia
- *Family Ischyromyidæ
  - None
- Family Aplodontiidæ
  - None recorded
- *Family Mylagaulidæ
  - None
- Family Sciuridæ
  - *Citellus*
- Family Castoridæ
  - *Castor*
- Family Heteromyidæ
  - **Cupidinimus?*
  - *Perognathus*
  - *Dipodomys*
- Family Geomyidæ
  - *Thomomys*
  - *Geomys*
  - *Cratogeomys*
- Family Cricetidæ
  - *Peromyscus*
  - *Onychomys*
  - *Sigmodon*
  - *Eligmodontia*
  - *Neotoma*
  - *Synaptomys*
  - *Ondatra*
  - **Mimomys*
- Family Zapodidæ
  - None recorded
- Family Erethizontidæ
  - *Erethizon*
- Family Caviidæ
  - None recorded

Lagomorpha
- Family Ochotonidæ
  - None recorded
- Family Leporidæ
  - **Hypolagus*
  - **Alilepus?*
  - *Lepus*

* Genus extinct.

Upper Pliocene extinct genera	4
Upper Pliocene living genera	16
Upper Pliocene sciuromorph genera	8
Upper Pliocene myomorph genera	8
Upper Pliocene hystricomorph genera	1

For the first time in the Tertiary of North America, myomorphs form an important element in the fauna. The ratio given above of one to one is probably in large measure accidental, but that there is a relative increase of myomorph genera cannot be doubted. A decrease of sciuromorph genera is also indicated, but this is fortuitous. Undoubtedly all Recent genera of Sciuromorpha were in existence by the end of the Pliocene, which would at least double the number indicated above.

An idea of the expansion of the myomorph element may be gained by recalling that all eight of the listed genera belong to one family, the Cricetidæ. The same family in the middle Pliocene has only two recorded representatives. Not only do the myomorph genera increase in number between the middle and upper Pliocene, but the number of

known specimens increases even more. Four myomorph genera are known from the lower and middle Pliocene. Of these, three are extinct and one living. The extinct genera are represented by a total of only four specimens. I do not know how many specimens of myomorphs are actually available from the lower and middle Pliocene, but from those I have seen, an estimate of less than two dozen would be warranted. Moreover, most of this material represents *Peromyscus*. The number of specimens in the California Institute collection of one upper Pliocene species alone, *Mimomys? parvus,* exceeds this figure. A specimen of *Mimomys* has even been found in an oil-well core. It must be remembered of course that most myomorphs are tiny animals, smaller than the average sciuromorph. It is natural to assume that these forms have often been overlooked in collecting. Also, the point should be raised that the small number of earlier Pliocene myomorph genera results from the limited amount of material available. Conversely, it might be argued that the larger number of upper Pliocene forms is directly due to the increased amount of material recovered from beds of this age. However, a number of small sciuromorphs have been found, and the factor of size would have little influence on the number of specimens of pre-upper Pliocene myomorphs as compared with upper Pliocene and Pleistocene types. In many cases the same individuals have made the collections from each of the horizons, and the collecting technique may be assumed to be approximately the same.

If, as it appears, therefore, a decided expansion of myomorph types occurred in upper Pliocene time, this fact may be employed in distinguishing the rodent faunas of the upper Pliocene from those of other stages of the Pliocene. The expansion is probably due to a combination of evolution and of migration from other regions.

The generally high percentage of sciuromorphs in the early Pliocene rodent faunas of North America stands in decided contrast to that in the faunas from the two adjoining continents, South America and Asia. The former continent possessed throughout the Pliocene an almost exclusively hystricomorph fauna. The Asiatic faunas, more particularly those of northern China and Mongolia, show a decided myomorph representation. The following rodent list from the upper Miocene and early Pliocene of Mongolia and northern China is given for comparison with the North American early Pliocene faunas. Some of the forms in this list are incorrectly determined, but this is relatively unimportant, since the purpose is to show the contrast in the major details of the fauna between Asia and North America. It is also possible that some upper Pliocene genera are included in this list. Genera that appear too doubtful have been omitted.

Asia (Upper Miocene and Early Pliocene)	North America (Early Pliocene)
Sciuromorpha	Sciuromorpha
Pseudaplodon	*Mylagaulus*
Tamius?	*Epigaulus*
Castor	*Liodontia*
Dipoides	*Sciurus*
Myomorpha	*Citellus*
Jerboas	*Marmota*
Paralactaga	*Eucastor*
Protalactaga	*Dipoides*
Alactaga?	*Castor*
Plesiodipus	*Perognathus*
Sicistids	*Perognathoides*
Heterosminthus	*Diprionomys*
Cricetids	*Cupidinimus*
Sinocricetus	*Thomomys*
Lophocricetus	*Pliosaccomys*
Microtodon	Myomorpha
Gerbillinæ	*Pliozapus*
Gerbillus	*Peromyscus*
Cape Rats	*Macrognathomys*
Prosiphneus	*Goniodontomys*
Siphneus	
Murines	
Acomys?	
Rhizomyidæ	
Pararhizomys	
Sciuromorph genera 4	Sciuromorph genera 15
Myomorph genera 13	Myomorph genera 4
Hystricomorph genera 0	Hystricomorph genera 0

A second distinctive feature of the upper Pliocene rodent faunas of North America as compared with earlier assemblages of the Pliocene lies in their modernization. Very few extinct genera are recorded, and, excepting the lagomorphs, even these are fairly close to modern types.

A number of upper Pliocene genera have no immediate ancestors in the North American Pliocene. Such genera are: *Sigmodon, Neotoma, Erethizon, Lepus, Alilepus?,* the microtine genera, and possibly *Eligmodontia.*

Pliocene *Sigmodon, Neotoma,* and *Eligmodontia* are found only in the San Pedro Valley fauna. It should be noted that this fauna has the most southerly position of any of the Pliocene rodent assemblages. Moreover, the above-named genera have at present a pronounced southern distribution. This statement is not true of *Neotoma,* but the genus is one of a number of genera which have such a distribution and are sometimes included in a separate subfamily, the Neotominæ. Several extinct South American rodents have also been included in

this group. It is doubtful whether the Neotominæ originated in any very southern locality, since the time available does not seem sufficient for an ancestral stock of the Neotominæ to have migrated southward and then returned. However, some such event may in part account for the lack of immediate ancestors of *Neotoma* in the early Pliocene of North America.

A species of *Sigmodon*, namely *atavus*, has been described by Schlosser (1924) from Mongolian Pliocene? beds. G. S. Miller (1927, pp. 17–19) stated that this supposed occurrence is an error and made Schlosser's species the type of a new genus, *Microtodon*, without affinities with *Sigmodon*. This view is more nearly in accord with the distributional evidence, and *Sigmodon* is probably to be considered an offshoot from some American *Peromyscus*-like stock.

The present southern distribution of *Eligmodontia* has been mentioned. The genus is sufficiently close to *Peromyscus* to have been derived from this form or its immediate predecessors before migration to South America, but what actually occurred is not known.

Erethizon is an undoubted derivative of a South American stock. The first appearance of the family in North America may be of considerable importance in Pliocene correlation.

Lepus and *Alilepus*, if the latter is properly referred to the Asiatic genus, were invaders from Asia. It seems likely that *Alilepus* was an earlier arrival than the modern hare. The first appearance of *Lepus*, in the author's opinion, is very close to the beginning of the Pleistocene as that period is defined in this paper.

The earliest undoubted record of *Lepus* in North America is in the San Pedro Valley faunas. *Lepus* can hardly be considered a derivative of *Hypolagus*, and presumably invaded this continent from the north during the later Cenozoic. The rapid extinction of *Hypolagus*, consequent upon the appearance of *Lepus*, is supported by the fact that in only one known fauna, the Anita, of lower(?) Pleistocene age, is there any association of the two genera. The Grand View assemblage is either latest Pliocene or Pleistocene. Equine remains from this fauna are very close to *Equus* and perhaps could be assigned as well to that genus as to *Plesippus*. *Hypolagus* is a member of this fauna, but no remains of *Lepus* are known. If *Lepus* had already arrived on this continent it should be recorded in this fauna, since the latter occupies a geographic position far to the north of the San Pedro Valley assemblages. If the Grand View assemblage is considered alone, the absence of *Lepus* may not possess great significance. However, the presence of *Hypolagus* and the absence of *Lepus* in the related Coso Mountains and Hagerman faunas strengthens the view that these assemblages antedate the appearance of *Lepus*. In this connection, the present wide distribution of *Lepus* should be borne in

mind. Judging from the almost universal presence of *Hypolagus* from the middle Miocene to upper Pliocene of the Great Basin and Pacific Coast provinces, the genus had a range approximately like the present distribution of *Lepus* in North America. It thus seems reasonable to suppose that the San Pedro Valley faunas, on the basis of lagomorph remains, are younger than that from Grand View.

It is of interest to note that Th. Kormos has recorded the genus *Hypolagus* from the Hungarian upper Pliocene (Kormos, 1934). In younger but still Pliocene strata, *Hypolagus* is found in association with sporadic occurrences of *Lepus*. In deposits containing still younger faunas, *Lepus* gradually replaces the more primitive form. Apparently no transitional types are known between the two genera. However, in Hungary *Hypolagus* seems to have prevailed somewhat later than in North America, unless the record results from a fuller European sequence of strata.

The San Pedro Valley fauna has been divided into two parts, an earlier fauna, the Benson, and a later one, the Curtis. *Lepus* is recorded in both. J. W. Gidley regarded the Benson fauna as of upper Pliocene age and slightly older than the Blanco; the Curtis fauna as slightly younger (Gidley, 1926, p. 83). Unfortunately, the only detailed descriptions of these faunas are of the rodents, lagomorphs, edentates, and proboscideans. Other forms have received only preliminary mention. Gidley records the presence of true *Equus*, *Lama*, Cf. *Pliauchenia*, Cf. *Procamelus*, *Odocoileus*, *Merycodus*, *Stegomastodon*, and *Glyptotherium* from the Curtis fauna. The Benson assemblage includes *Pliohippus*, *Hipparion*, Cf. *Pliauchenia*, Cf. *Procamelus*, *Platygonus*, *Merycodus*, and *Anancus*. It should be recalled that both faunas occupy apparently the same stratigraphic position in the San Pedro Valley beds. The Curtis fauna possesses some forms which may be Pleistocene. The anomalous presence of *Merycodus* and of other types suggests that there has been a reworking of the material in the deposit, and that part of the fauna is indeed Pleistocene, thus agreeing with the evidence furnished by the presence of *Lepus*. If this is true for the Curtis locality, a similar circumstance may account for the presence of *Lepus* in the Benson fauna. Accordingly, the view might be held that two faunas are present, an upper Pliocene assemblage equivalent to or slightly older than the Blanco, and a Pleistocene fauna. I have not examined material from the Benson locality, but that of the Curtis fauna in the California Institute collections is very fragmentary and is not incompatible with the view of reworking. However, the rodent faunas from the two localities indicate no great separation in time. Moreover, Gidley's description of the occurrence and the rather complete preservation in some cases seemingly argue against any mixing on a large scale.

In view of their southerly location, the San Pedro Valley faunas may appear slightly older than they actually are. This suggestion, however, is again inadequate to explain entirely the stage of evolution presented by some of the forms. The author, of course, is here concerned only with the presence of *Lepus* in the faunas. The Rodentia could be upper Pliocene, but not older. Perhaps the hares are not typical members of either fauna and have been introduced by some means not determined.

The final solution of the problem offered by the San Pedro Valley faunas must await detailed description of the remaining elements of the assemblages, which may alter the present determinations to some extent, and perhaps more detailed geologic examination of the beds. For the present, the faunas present an obstacle to the acceptance of the view that *Lepus* is exclusively Pleistocene in age.[1]

Summary of Upper Pliocene Rodent Faunas

The principal characteristics of upper Pliocene rodent faunas are as follows:

1. Sharp faunal break from the middle Pliocene as evidenced by: (a) decided increase in myomorph population; (b) decided decrease in number of extinct genera; (c) first appearance of many modern types.
2. No Mylagaulidæ.
3. Presence of the genus *Mimomys*, as well as the relative abundance of microtines.
4. No *Dipoides*, nor at present any known representative of the *Eucastor-Dipoides* line.
5. Absence of *Lepus*, except perhaps in final(?) faunal stages.
6. First appearance of typical *Citellus*.
7. First appearance of hystricomorphs(?).
8. All species probably extinct.

Ecology of Upper Pliocene Faunas

The Grand View, Hagerman, Benson, and Curtis faunas are the only upper Pliocene rodent assemblages complete enough to afford much evidence as to the ecologic conditions during the upper Plio-

[1] Since the present report was written I have been informed by Dr. C. L. Gazin that *Hypolagus* is present in the Benson fauna. This information caused me to realize that I had been uncritical in accepting Dr. Gidley's identification of the Benson lagomorphs. A reinvestigation of the fauna suggests that specimen No. 10529, or at least a $P\overline{3}$ referred to this number, identified by Gidley as *Sylvilagus* or *Brachylagus* sp., represents a *Hypolagus*. Moreover, the specimens referred to *Lepus* are hardly adequate to demonstrate definitely the presence of jack-rabbits in the Benson assemblage. However, *Lepus* is present in the Curtis fauna, and the rodent and lagomorph assemblages from the Benson and Curtis localities apparently are sufficiently related so that the above discussion is not rendered pointless by any changes in identification which may be made in the future.

cene. These faunas fall into two groups both geographically and ecologically. The Grand View and Hagerman faunas suggest the close proximity of fresh water and the general prevalence of rather moist conditions with abundant grasses. Moreover, the presence of voles and especially of lemmings indicates perhaps a relatively cool climate. Lemmings in general point to a boreal climate. Hence their presence in the Grand View fauna might suggest proximity to the Glacial Period or to a time of actual glaciation of the continents. It must be pointed out, however, that *Synaptomys* extends today into the upper Austral zone, its range reaching as far south as North Carolina, Tennessee, and Arkansas. Further, its range may have been less restricted in the upper Pliocene. The Benson and Curtis faunas, on the other hand, suggest, in the presence of *Dipodomys, Onychomys,* and *Perognathus,* assemblages that existed under arid or semiarid conditions. The presence of *Sigmodon* and *Neofiber?* suggests that areas of a moister environment were also present. On the whole, the Grand View and Hagerman assemblages point to a cool, rather moist climatic condition, and the San Pedro Valley fauna to a warm, drier environment.

During the earlier Pliocene there was a gradual increase in hypsodonty of the cheek-teeth in many rodent types. This change seems to be abruptly accelerated in the upper Pliocene. The coming of glacial conditions may account for the appearance of such forms as the microtines, and the increasing aridity for the appearance of *Dipodomys* and similar types.

CORRELATION OF PLIOCENE RODENT FAUNAS

It should be indicated at the outset that the correlations made in this section are tentative. Many of the rodent faunas are small and incompletely known. Faunas of identical age may have few or no forms in common as a result of varying environmental conditions or of fortuitous collecting, since the Rodentia show great differentiation. It would be quite surprising if all the exact correlations were correct. Perhaps such correlations, in view of the scanty evidence, should not be made. However, in some cases the larger mammals associated with the rodents have not been studied in detail and the relative position of the fossil assemblages is not known. Hence, if in the last analysis the attempted correlations are proved correct, the fact may demonstrate the value of fragmentary remains of rodents in determining stratigraphic relationships.

It seems fairly well established that the known Pliocene rodent faunas may be divided primarily into three groups corresponding in age to the lower, middle, and upper divisions of the Pliocene as recognized in this paper. The characteristics of these stages have been set forth in the preceding section. A fourth and youngest stage, charac-

terized by the presence of *Lepus*, may also be present. If this actually exists, it might best be referred to the lower Pleistocene.

Not enough attention has been given in recent years to the Pleistocene rodent assemblages to furnish a basis for recognition of faunal stages within this epoch. If valid inferences are to be drawn from what is known, as well as from the character of the upper Pliocene fauna, the lower Pleistocene should be characterized by (1) the presence of *Lepus* among the lagomorphs, and (2) the presence of principally extinct species, readily recognizable as such. This stage is possibly represented by one or both of the San Pedro Valley faunas, and the Anita, Arizona, fissure accumulation described by Hay (1921). Theoretically, at least, the middle Pleistocene should yield a mixture of living types of rodents and those definitely extinct. Some of the eastern wet-cave faunas appear referable to this age. Recently, Lugn and Schultz (1934) have referred the "Sheridan beds" and the Hay Springs Quarry fauna tentatively to the middle Pleistocene. Upper Pleistocene rodent faunas comprise only existing species, or if any are extinct they are closely allied to living forms. However, exception to this statement must be made if the genus is extinct, as may be the case whenever the aberrant *Castoroides* is present. The most completely known upper Pleistocene assemblages are those of the California tar-pits. The age of the tar-pit faunas has been a subject of much discussion. At first, Rancho La Brea was regarded as representative of the Aftonian interglacial stage. Later work has tended to transfer this assemblage to the upper Pleistocene, and the rodent faunas of this and similar occurrences strongly suggest also a late stage in Pleistocene time.

If some or all of the more typical upper Pliocene faunas are eventually placed in the Pleistocene, this will serve only to move up the Pleistocene faunas without changing their relative positions. In this event, the first appearance of *Lepus* in the faunas would not coincide with the beginning of the Pleistocene but with a later but still lower Pleistocene stage.

Certain Pliocene rodent faunas have been omitted from the discussion either because they are very fragmentary or because the present author is not familiar with them. The following assemblages are discussed in this section: Fish Lake Valley, Siesta, Kern River, Rattlesnake, Rome, Smiths Valley, Thousand Creek, upper Etchegoin, Coso Mountains, Hagerman, Grand View, Benson, and Curtis. These faunas fall more or less readily into one or another of the three main faunal stages established in this paper.

LOWER PLIOCENE

The Siesta and Fish Lake Valley rodent faunas are characteristic of the lower Pliocene. The Siesta is so poorly known that it would be

omitted except for the fact that the beds furnish material representing *Eucastor,* one of the most useful rodent types in Pliocene correlations. The species, *E. lecontei,* is clearly more advanced than that from Fish Lake Valley, and less advanced than *Dipoides* from the middle Pliocene. For this reason the Siesta is placed above the Fish Lake Valley fauna and below the mid-Pliocene assemblages.

The Fish Lake Valley or Esmeralda fauna is the most primitive of the rodent faunas dealt with in this section. Not only is it characterized by the most primitive known species of *Eucastor,* but *Peromyscus dentalis,* from this fauna, is distinctly more primitive than mid-Pliocene species. Moreover, the Fish Lake Valley heteromyids appear to be closely related to forms from the Barstow. The fauna would be considered Miocene by some palæontologists. The author has no preference in the assignment of this assemblage to either the lower Pliocene or the upper Miocene, but the appearance of the genus *Eucastor* is a convenient Pliocene marker. The Equidæ from the Fish Lake Valley fauna include the genus *Hipparion,* which is still considered a "signpost" of the Pliocene by most workers.

MIDDLE PLIOCENE

The following faunas appear to be of middle Pliocene age: Rattlesnake, Kern River, Smiths Valley, Thousand Creek, and Rome. The relative position of these faunas with regard to one another is uncertain.

A species of *Dipoides* is recorded from the Rattlesnake. This species is apparently less advanced than *D. stirtoni* of the Rome fauna. For this reason, the Rattlesnake is considered as slightly older than the Rome rodent fauna. The scarcity of rodent material, including that of *Dipoides,* in the Rattlesnake collections prevents any very reliable age determination on the basis of the Rodentia. If the Rome rodent assemblage is at least as advanced as that from Thousand Creek, then the available material from the Rattlesnake supports the general opinion that the Rattlesnake is somewhat older than the Thousand Creek.

The Thousand Creek rodents comprise the largest and most complete assemblage among the middle Pliocene faunas. Fragmentary remains of *Dipoides* represented in the assemblage may be identical with *D. stirtoni,* but it is impossible to make this determination with certainty. A large species of *Peromyscus, P. antiquus,* is also recorded. The Thousand Creek rodent fauna may be slightly older than that from Rome. This is suggested by the presence in the latter of *Castor* and a microtine genus, *Goniodontomys.* These forms are more characteristic of the upper than of the middle Pliocene, and perhaps point to a younger age for the Rome fauna. However, these animals

are rare in the Rome collection, and their absence in that from Thousand Creek may be fortuitous or due to the presence of somewhat different environmental conditions. Study of the Rome assemblage as a whole has not been extended sufficiently to determine the exact relationships of this fauna other than to establish for it an age comparable to that of the Rattlesnake–Thousand Creek.

The Smiths Valley rodent fauna is tentatively regarded as approximately contemporaneous with, or slightly older than, the Thousand Creek fauna. Practically identical species of *Peromyscus* are found at both localities. The cotype of *Cupidinimus magnus* from the Thousand Creek exhibits a certain resemblance to the Smiths Valley *Pliosaccomys*. If specific identity could be established, similarity of the two faunas would be strengthened. However, the relation of these rodent types cannot be satisfactorily determined with the existing Thousand Creek material. As a matter of fact, they are referred to separate families.

No especially diagnostic forms are known from the Kern River. Presence of a large species of *Peromyscus* is regarded by the author as indicative of a middle Pliocene age. Owing, however, to the incomplete character of the rodent remains, an age assignment to this fauna becomes largely dependent upon evidence furnished by the larger mammals. As a matter of fact, owing to the fragmentary nature of most rodent faunas, more or less use is made of other lines of evidence in arriving at age determinations. If rodent assemblages offer evidence concerning relative ages of faunas, I have not hesitated to use this in preference to other data, but in its absence I have fallen back on the usually accepted testimony of the larger mammals.

UPPER PLIOCENE

The upper Pliocene rodent faunas included in this discussion are: upper Etchegoin, Coso Mountains, Hagerman, Grand View, Benson, and Curtis. The latter four are the only faunas of any considerable size. Unfortunately, the Hagerman–Grand View faunas differ so much in type from the Benson-Curtis assemblages that comparisons are quite limited. I have placed the Idaho faunas as slightly older than those from Arizona, chiefly because the latter are characterized by the presence of *Lepus*, the former by *Hypolagus*.

The Grand View mammalian assemblage appears to be slightly younger than that from Hagerman. Rodent forms suggesting this difference in age are *Mimomys primus*, present in the Hagerman fauna but absent in the Grand View, and species of *Ondatra*. *Ondatra* from Grand View may be slightly advanced over that from the older locality.

The rodent faunas of the Curtis and Benson are quite close to each other. A slight difference in age may be indicated in certain instances, in which cases the Benson fauna appears to be the older. The only extinct genus recorded from either assemblage is from the Benson. If a genus is represented in both faunas, the species are usually distinct, with some evidence that the Benson species are slightly less advanced. However, among rodents there does not seem to be the anomalous association of advanced and primitive types found among the larger mammals.

The Coso Mountains fauna is tentatively correlated with the Hagerman, since two of its types, a vole and a lagomorph, are probably identical with Hagerman species.

Only two rodent forms are known from the upper Etchegoin or San Joaquin clay. Deposition of the San Joaquin clay apparently represents a considerable period of time, and as the rodent types are separated stratigraphically as well as geographically, the "fauna" cannot be correlated exactly with any of the related upper Pliocene assemblages. One of the types occurring here, namely *Mimomys primus*, may be regarded tentatively as of the same age as the Coso Mountains and Hagerman faunas. The second rodent, *Castor californicus*, according to Stirton, is somewhat more primitive than the Hagerman beavers, and this fact suggests an age determination of the beds in which it occurs as slightly older than that of the Hagerman fauna.

It is quite possible that some of the faunas here referred to the upper Pliocene are actually lower Pleistocene. The possibility of this in connection with the San Pedro Valley assemblages has already been mentioned. The Grand View fauna may also be more appropriately placed in the Quaternary. Indeed, if views on the Pliocene-Pleistocene boundary expressed by several workers in the past ten years are applied to the faunas under discussion, most or all of them would be transferred to the Pleistocene.

Barbat and Galloway (1934, pp. 494–498) in a paper on the San Joaquin clay (upper Etchegoin) place the strata (zone "B" of these authors) in which *Mimomys primus* occurs in the lower Pleistocene. *Castor californicus* apparently is from their zone "C," which is designated lower Pleistocene, or transitional between the Pliocene and Pleistocene. They tentatively correlate zone "C" with the Cromer Forest Bed [1] and the Las Posas (first interglacial of California). Zone "B" was correlated with the Timm's Point of Southern California and the Mindelian glaciation of Europe. If Barbat and Galloway are correct in these tentative correlations, almost all of our upper Pliocene

[1] P. G. H. Boswell, in Proc. Geol. Assoc., 87–111, 1931, maintains that reference of the Weybourne Crag to a glacial stage or of the Cromer Forest Bed to a warm period is incorrect.

faunas could be placed in the lower Pleistocene. Even these authors leave the first glacial period (San Joaquin clay, zones "D" and "E"; Günz glaciation of Europe) in the upper Pliocene. According to the definition of the Pleistocene adopted by the United States Geological Survey, this stage should also be placed in the Quaternary. E. Haug has maintained this view in Europe, although most European palæontologists still include the first glaciation in the Pliocene.

The nearest equivalents in Europe of the Hagerman, Coso Mountains, and related faunas appear to be the Norwich Crag and Val d'Arno.[1] The latter are generally referred to the upper Pliocene, but also are usually considered as contemporaneous with the Günz glaciation. Thus according to American standards these faunas are of Pleistocene age, a view according to Matthew (1929, pp. 438–439) and Hay (1925, p. 240) that now finds other European supporters besides Haug.

One last point needs to be touched upon. It seems hardly likely that *Mimomys primus* occurs in a faunal stage which can be correlated with the Mindelian glaciation. *M. primus* is closest in characters to *M. pliocœnicus* of Europe. This latter species is typical of the Norwich Crag and extends no higher than the lower Cromerian. The genus *Mimomys* may extend into the Mindelian, but the various species in the European deposits are relatively short-lived. In view of the latter fact, it may be assumed, in absence of knowledge to the contrary, that the American species also had a limited range in time. Hence, since *M. primus* is somewhat more primitive than *M. pliocœnicus,* and this form in turn is in many ways the most primitive of known European representatives of the genus, it is improbable that the assignment of zone "B" to the Mindelian is correct unless a considerable homotaxial element enters into these relationships. However, I do not wish to imply that a genus of mammal or even an entire fauna is sufficient in the present state of our knowledge to permit intercontinental correlation involving such short periods of time as those represented by glacial and interglacial stages. Even the correlation of the North American upper Pliocene faunas with those of Europe that have been suggested in this paper may not be countenanced by many palæontologists. Correlation of a series of temperature changes for the Pleistocene on this continent with a similar series in Europe may be possible, with consequent establishment of rather exact time relations, but it should be mentioned that a solution of a similar problem presented by the Pleistocene of the British Isles and that of the European continent has not been reached with great success (Evans and Stubblefield, 1929, p. 498).

[1] These European faunas do not appear comparable to our own "early Pleistocene" (*i.e.,* Sheridan and equivalents), as W. D. Matthew believed.

Pliocene glaciation may account in part for the marked change in rodent faunas in the upper Pliocene, noted on previous pages. This change is sharper than any succeeding one, and from this standpoint the rodent assemblages now regarded as of the upper Pliocene might be more conveniently placed in the Pleistocene. In either case, it seems likely that some of the upper Pliocene rodent faunas discussed in the present paper belong to a period embraced by the first glacial and interglacial stages. This point is interesting since it has been maintained by some that the famous Rancho La Brea assemblage is Aftonian (first interglacial). As it is obvious that the faunas under discussion are in no way equivalent to Rancho La Brea, they furnish an additional reason for believing that the brea deposits are upper Pleistocene in age. This point has been mentioned before, but it bears repeating, since it applies not only to Rancho La Brea but to other deposits of similar faunal stage which have been referred to the lower Pleistocene.

Wherever the dividing line between Pliocene and Pleistocene may be drawn ultimately, the relative positions of the faunas are not altered. For this reason, and pending a fuller treatment of the subject by Mr. J. R. Schultz, the author prefers to keep the upper Pliocene rodent faunas where they are usually placed. The following chart (fig. 2) presents a tentative correlation of some Pliocene faunas based on a study of their rodent assemblages.

	Pacific Coast Province	Great Basin Province	
		California	Arizona, Nevada, Oregon, Idaho
Upper	Upper Etchegoin ↕ { Mimomys / Castor }	Coso Mountains	Curtis Benson Grand View Hagerman
Middle	Kern River?		Rome Thousand Creek–Smiths Valley Rattlesnake
Lower	Siesta		Fish Lake Valley

FIG. 2—Correlation chart showing time relationships of Pliocene rodent faunas

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